Red-tree vole habitat suitability modeling: Implications for conservation and management

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ABSTRACT

In the Pacific Northwest, USA, red-tree voles (*Arborimus longicaudus*) are of conservation and management interest owing to their apparent association with late-seral forests and the relatively small extent of such forests, largely a function of timber harvest, fire, and conversion of forests to non-forest uses during the past century. We created and evaluated a series of red-tree vole habitat association models, and applied the best model to evaluate tree vole habitat quality within and outside of reserves throughout most of their range in Oregon and northern California. We modeled presence and absence of tree vole nests across a gradient of biotic, abiotic, and spatial features; and within and outside of reserves. The best model included spatial coordinates, percent slope, basal area of trees with diameter at breast height (dbh) between 45 and 90 cm, maximum tree dbh, and standard deviation of conifer dbh. Plots with tree vole nests contained many late-seral/old-growth forest attributes such as large diameter, older, and variably sized trees. Evaluation of the best model, including rigorous cross-validation, showed the model to be statistically robust and to have very good/excellent predictive ability. Reserves had significantly higher mean habitat quality than non-reserved lands, and reserves had much more high quality habitat than non-reserves.

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1. Introduction

Tree voles (*Arborimus* spp.) are the most specialized voles in the world (Maser et al., 1981) and yet one of the most poorly understood mammals endemic to the temperate forests of the United States' Pacific Northwest (Forsman et al., 2004). Several life history traits may limit the ability of tree voles to withstand timber harvesting practices which often create fragmented landscapes characterized by young forests (Huff et al., 1992; Biswell and Forsman, 1999; Forsman et al., 2004). Tree voles: (1) live in conifer forests and forage on conifer leaves (Taylor, 1915; Howell, 1926; Benson and Borell, 1931); (2) have exceptionally long gestation periods, small litters, and slow juvenile growth rates (Hamilton, 1962); (3) have a relatively small geographic range (Johnson and George, 1991); (4) have limited dispersal abilities (Biswell et al., 2000; Swingle, 2005). Although tree voles do occur in young forests (Taylor, 1915; Howell, 1926; Benson and Borell, 1931; Maser, 1966; Thompson and Diller, 2002; Swingle, 2005), many research-

ers have suggested that they are habitat specialists primarily associated with mature and old forests (Corn and Bury, 1986; Raphael, 1988; Carey, 1989; Aubry et al., 1991; Gilbert and Allwine, 1991; Ruggiero et al., 1991; Gomez and Anthony, 1998; Biswell and Forsman, 1999; Jones, 2003). Carey (1991) and Huff et al. (1992) suggested that tree vole populations in young forests were not self-sustaining, and that such habitats were population sinks. In contrast, Swingle (2005), cautioned against the blanket assumption that young forests are always population sinks and urged managers to consider young forests as potential habitat for tree voles, especially in areas where old forests are rare. Despite research efforts, uncertainty still exists regarding basic ecological questions, namely their distribution and relative abundance in different forest types across their relatively small geographic range (Forsman et al., 2004).

There are two tree vole species, the Sonoma tree vole (*Arborimus pomo*) in California and the red-tree vole (*Arborimus longicaudus*) in Oregon and northern California (Johnson and George, 1991; Bellinger et al., 2005). The boundary between the two species is approximately the Klamath River in northern California, but the exact boundary and taxonomic relationships between the two species are still not fully resolved (Johnson and George, 1991; Bellinger et al., 2005; Miller et al., 2006). Although morphological and genetic distinctions exist between these two

species, no apparent ecological differences have been discovered (Johnson and George, 1991; Smith et al., 2003).

The general lack of information on tree vole biology, their relatively uncommon occurrence in young forests, and concern that forest fragmentation would lead to the development of isolated subpopulations all contributed to their being listed as a "Survey and Manage" (hereafter SM) species under the Northwest Forest Plan (USDA/USDI, 1994; hereafter NWFP). The NWFP was an unprecedented attempt by the federal government in the U.S. to manage ∼10 million ha of federal land in Washington, Oregon, and northern California as an ecosystem (USDA/USDI, 1994). The red-tree vole was one of >400 species, and the only mammal, initially listed as a SM species. The SM provisions attempted to protect taxa that were believed to: (1) occur within the NWFP area; (2) be associated with late-seral/old-growth forests; (3) not be adequately protected within the reserve system set up under the NWFP, a system designed largely using quantitative data on the northern spotted owl (*Strix occidentalis caurina*) and qualitative data and expert opinion on >1000 other species. The second and third assumptions were not specifically tested prior to listing any species as SM, but expert opinion and, when available, scientific information informed the listing process. Prior to on-the-ground management activities (e.g., timber harvest, road removal, controlled fire), land managers were often required to *survey* for SM species, and to *manage* for their continued occurrence if they were found (USDA/USDI, 1994). Finding, monitoring, and managing for rare, cryptic, and elusive species is extremely difficult and expensive (Raphael and Molina, 2007). Furthermore, the relatively small spatial scale of most studies limits the area to which scientifically valid inferences can be drawn. Lastly, study-specific measurements (e.g., the suite of biotic and/or abiotic features that are estimated) and protocols, often prohibits direct application of research findings by land managers.

To address these difficulties and shortcomings, we sampled for red-tree vole (hereafter, RTV) nests across most of their range, including the potential zone of overlap between *A. longicaudus* and *A. pomo* in northern California. Sample sites were co-located at pre-existing plots at which vegetation data are routinely collected (see Section 2). We modeled the presence–absence of RTV nests at these sites, and extrapolated the model to all plots at which vegetation data existed within the range of the RTV. In order to quantify the value of the NWFP reserves to tree voles, we evaluated the quality of RTV habitat in reserved and non-reserved lands. We provide a quantitative method for monitoring RTV habitat quality and distribution over time (by applying our model to the plots that are periodically re-sampled), and a quantitative evaluation of two of three SM criteria: the species' presumed association with late-seral/old-growth forests, and an evaluation of the habitat value within reserved and non-reserved lands. In part, this last evaluation is an indication of the value of the northern spotted owl as an umbrella species (Dunk et al., 2006).

2. Methods

2.1. Study area

The study area included approximately 2.7 million ha of land in western Oregon and northern California. It included nearly the entire range of the *A. longicaudus* except for portions of the northern Coast Ranges and northern Cascades in Oregon (Fig. 1). The study area included forest lands sampled in the following physiographic regions: Oregon Coast Range, Middle Cascade Mountains, and the Klamath Mountains in Oregon and California, and the Coast Range in California. Generally, areas near the coast are cooler year-round, with more extreme summer highs and winter lows along west to east gradients. Similarly, general

gradients from more xeric to more mesic conditions exist from south to north.

Topography throughout the study area is generally steep and rugged. Land use history is quite varied, with large areas of intensive silviculture operations and large areas of reserved lands with little-to-no evidence of silvicultural operations. Similarly, forest structure and age varied dramatically, ranging from recently logged areas to 600-year-old structurally complex forests that have never been logged.

2.2. Vegetation data

We acquired vegetation data from 1003 Current Vegetation Survey (CVS) and Forest Inventory and Analysis (FIA) plots within the range of the RTV (USDA, 2001a,b; http://www.fs.fed.us/r6/survey/document.htm; http://www.fs.fed.us/pnw/fia/publications/fieldmanuals.shtml). These plots are systematically spaced on Federal lands at intervals of ∼2.7 km in Oregon and ∼5.5 km in California (Fig. 1), and are re-sampled every 10 years to monitor regional changes in vegetation (USDA, 2001a,b). Standardized physiographic and physiognomic information was collected at each site, creating an extensive database available to land managers for monitoring changes on the landscape in response to management practices and natural phenomena.

Although many vegetation variables are measured at CVS/FIA plots (USDA, 2001a,b; http://www.fs.fed.us/r6/survey/document.htm; http://www.fs.fed.us/pnw/fia/publications/fieldmanuals.shtml), we extracted only those variables known or suspected to be important to tree voles. We evaluated published and unpublished papers, spoke with field researchers, and used our own field experience with the species to identify variables used in the analyses. Only plot-level data were used to estimate biotic variables.

2.3. Estimating red-tree vole nest presence and abundance

From the 1003 CVS/FIA plots on Federal lands within the range of the RTV, a spatially balanced stratified random sample of 400 plots were selected in which the number of trees containing tree vole nests was estimated (Rittenhouse et al., 2002). Ultimately 368 of these plots were sampled for voles, with 32 plots being eliminated because of logistical or safety reasons. Plots were stratified based on habitat (late-successional and old-growth forests [LSOG] vs. non-LSOG) and whether the plot fell within a reserve or not. LSOG status was determined based on mean tree age >80 years. Allocation of plots by LSOG/non-LSOG and reserve/non-reserve was as follows: reserve/LSOG = 60%, reserve/non-LSOG = 20%, non-reserve/LSOG = 10%, and non-reserve/non-LSOG = 10%. Our goal was to evaluate red-tree vole habitat associations via the development and testing of multiple competing models, which we are reporting here. Of 368 sampled plots, we were able to use FIA/CVS data from 365 plots (data were unavailable for 3 plots).

RTV surveys were conducted between October 2001 and October 2004. Within each square 1-ha plot, at least two trained observers conducted visual searches for tree vole nests while walking along four transects that were spaced 25 m apart. When either fecal pellets, resin ducts, or potential nests were observed, vole nests were confirmed by climbing trees and examining all potential nests to see if they contained evidence of occupancy by tree voles (fecal pellets, resin ducts, and confer branch cuttings). A major concern with ground-based surveys of tree vole nests is that significant numbers of nests may go undetected, especially in old forests where many nests are so high in the canopy that they cannot be detected from the ground (Swingle, 2005). Therefore, to reduce the number of false negatives (no vole nests detected in a
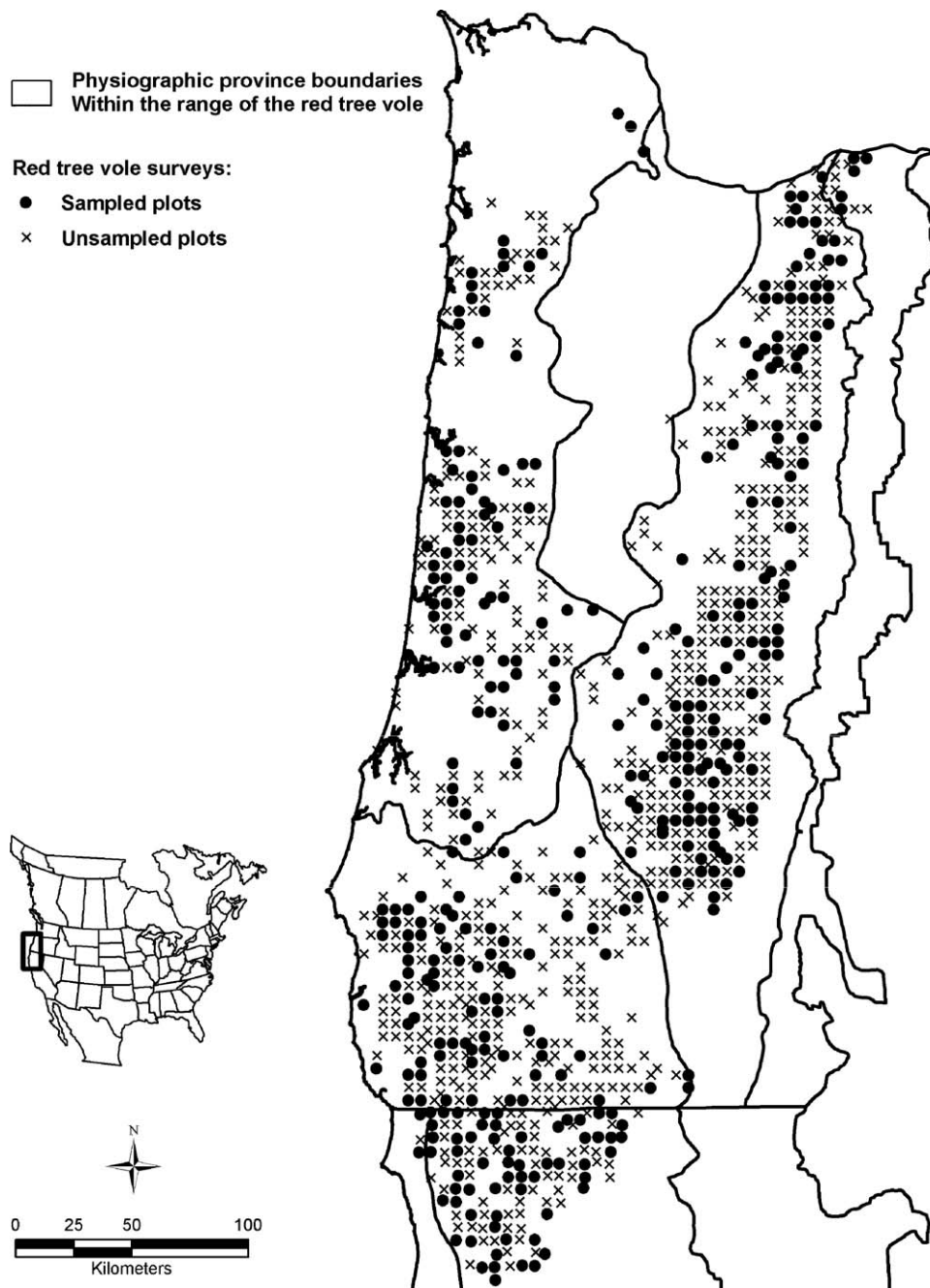
Fig. 1. Study area boundary and plot locations.

plot when nests were actually present), surveyors also climbed a stratified random sample of five Douglas-fir (*Pseudotsuga menziesii*) trees in those plots where (1) no nests were detected from the ground and overstory trees were >61 cm diameter at breast height (dbh), or (2) tree canopies were judged to be too large or dense to be effectively surveyed from the ground. Stratified random samples included 2 trees that were 61–91.5 cm dbh and 3 trees >91.5 cm dbh. Trees of other size classes and species were climbed if trees meeting the above criteria were unavailable. Total number of RTV nests detected was recorded at each plot. For our *modeling*, however, only presence or absence of RTV nests was used. For *evaluating* the habitat value of reserves and non-reserves, we also used number of nests detected (see below). Presence was defined as having at least 1 RTV nest, occupied or not. Absence was defined as no tree vole nests detected.

2.4. Analyses

We used an information-theoretic approach to model development and selection (Burnham and Anderson, 2002). We compared ~200 *a priori* habitat association models. Approximately 67 base models were slightly changed by substituting highly correlated variables (e.g., diameter of largest Douglas fir vs. largest tree diameter) during three iterations. Models were created based on RTV literature, field experience, and a series of late-seral forest models we developed. We used vegetation and topographic data from FIA/CVS plots and their UTM coordinates as predictor variables. UTM coordinates were included to examine the spatial structure of tree vole detections. For species like red-tree voles that do not disperse long distances it could be that high quality habitat exists outside of areas that are currently occupied owing to their

lack of dispersal ability (including formerly occupied areas of a geographic range). We used combinations of 23 variables to create *a priori* models consisting of 1–7 variables. Models were ranked using bias-corrected Akaike's Information Criterion (AIC$_c$; see Burnham and Anderson, 2002). We also calculated Akaike weights and relative likelihood of the best model compared to all other models.

We used logistic regression with generalized additive models to estimate the probability that RTV nests would be present (Po; see Dunk et al., 2004; Welsh et al., 2006; Zielinski et al., 2006 for details of using this analytical approach) at FIA/CVS plots. We tested for spatial autocorrelation in the best model's residuals using Moran's I with a distance interval of 15-km. The best model identified by AIC$_c$ was subsequently evaluated by estimating: (1) Area Under the Curve (AUC) using Receiver Operating Characteristic (ROC) curves (see Fielding and Bell, 1997); (2) Cohen's kappa (Cohen, 1960; Manel et al., 2001); (3) percentage of observations that were correctly classified. We attempted to optimize correct classification of presence/absence sites by evaluating a series of probability thresholds for classifying plots as having RTV nest(s) present or absent. Due to RTV's status in the study area (i.e., assumed to be a relatively rare habitat specialist), we wanted to avoid the possible bias of correctly predicted absence sites on the overall (total) correct classification, at the expense of presence sites. Subsequently we conducted a 10-fold cross-validation exercise to assess the robustness of the full-dataset model (see Fielding and Bell, 1997). Each of 10 times, we randomly selected 15% of the observations (test data) and used the remaining 85% (training data) to create a model, and then classified the test data with that model. Test data from the 10-fold cross-validation procedure were compared to the original full-dataset model's performance using the same evaluation procedures identified above.

2.5. Evaluating strength of selection/habitat quality

The best model was then used to predict the probability that RTV nests would be present at each of the 1003 FIA/CVS plot locations. Because the study design emphasized sampling plots classified as "LSOG" and plots falling within reserves, sampled plots were not completely representative of the population of plots from which the sample was drawn. Therefore, we utilized estimates of Po for the entire population of 1003 plots to estimate the distribution and abundance of habitat quality within 10 equally sized bins (see Boyce et al., 2002; Hirzel et al., 2006) from 0 to 1. Following Hirzel et al. (2006) we divided the percentage of sampled plots at which RTV nests were detected within each bin by the percentage of the study area estimated to occur within that bin. The resulting predicted-to-expected ratio (sensu Hirzel et al., 2006) was an index to the strength of selection by RTV (<1 = avoidance, >1 = selection) and/or relative habitat quality. If the best model's predictions represent a gradient from lowest to highest value habitat, RTV should show stronger selection for higher-value bins and weaker selection for low-value bins, and we should see a strong, positive relationship between bin-rank (or mean bin value) and strength of selection (Hirzel et al., 2006).

2.6. Evaluating reserved and non-reserved lands

We compared the predicted habitat value of reserved land plots and non-reserved land plots by extrapolating the best model to both sampled and un-sampled FIA/CVS plots within the study area (*n* = 564 plots in reserved lands and 439 plots in non-reserved lands). We then used a two-sample *t*-test to evaluate differences in estimated mean Po values (mean RTV habitat quality) for plots in reserved vs. non-reserved lands. We also evaluated the distribution of habitat qualities within reserved and non-reserved lands; using the 10 equal-sized bins described above.

In order to provide useful information for the on-the-ground conservation and management of RTV, we divided estimated Po values into four equal bins ranging from 0 to 1. Within each bin we calculated the mean and standard error for all biotic variables we evaluated. This was an attempt to evaluate patterns of change in each variable (not only those in the best model) as relative habitat quality changed. We also evaluated how number of RTV nests in each plot varied within each of the four Po bins. If RTV habitat quality increases with increasing bin rank, we should expect more nests to be found in higher quality habitat. We used chi-square goodness of fit to evaluate whether four categories of nest abundance (0, 1, 2–3, and ≥4 nests) were randomly distributed among the four Po bins. We combined plots with 2–3 nests and those with ≥4 to increase sample sizes in each group. In all analyses "presence" was based on all RTV nests detected, regardless of whether the nests were old dilapidated nests or nests with evidence of recent occupancy.

3. Results

Trees containing RTV nests were detected at 96 of 365 plots surveyed, including 44 plots with 1 nest tree, 30 plots with 2–3 nest trees, and 22 plots with ≥4 nest trees. Univariate comparisons of plots at which RTV nests were detected vs. those at which they were not detected revealed some large differences (Table 1). Most different were several attributes correlated with old-growth forests including: volume of downed large woody debris (~2.5 times more volume in plots with RTV nests), basal area of trees with dbh >90 cm (~2.3 times more in plots with RTV nests), basal area of trees with dbh >45 cm (~1.6 times more in plots with RTV nests), mean dbh of Douglas-fir trees (~1.5 times larger in plots with RTV nests), standard deviation of dbh of conifers (~1.5 times greater in plots with RTV nests), maximum diameter of Douglas-fir trees (~1.46 times larger in plots with RTV nests), and mean tree age (~1.3 times older in plots with RTV nests).

3.1. Model selection and evaluation

The model that best fit the data included the interaction of UTM easting and UTM northing, percent slope, basal area of trees with dbh = 45–90 cm, maximum tree dbh, and standard deviation of conifer dbh. This model represented 94.7% of the cumulative weights of all models. Therefore, we did not conduct any model averaging. The form of the relationship between probability of

Table 1
Univariate comparisons of variables in plots at which red-tree vole nests were found and those at which nests were not found. SD = standard deviation.

	Nest detected		Nest not detected	
	Mean	SD	Mean	SD
Large downed wood (m³/ha)	61	157	24	76
Basal area >90 cm dbh (m²/ha)	23	18	10	14
Basal area >45 cm dbh (m2/ha)	41	22	26	23
Mean dbh Douglas fir (cm)	70	31	45	29
SD dbh conifers[a] (cm)	26	8	18	9
Maximum dbh Douglas-fir (cm)	144	39	98	48
Mean dbh five largest trees (cm)	123	34	86	37
Maximum tree dbh[a] (cm)	149	37	108	40
Mean tree age (years)	153	72	120	65
Total basal area (m²/ha)	54	22	43	24
Basal area trees 45–90 cm dbh[a] (m²/ha)	19	10	16	15
Mean conifer dbh (cm)	42	17	37	18
Percent slope[a]	51	22	45	22
Elevation (m)	628	338	838	396

Mean (and SD) of [a]UTM coordinates are not included.
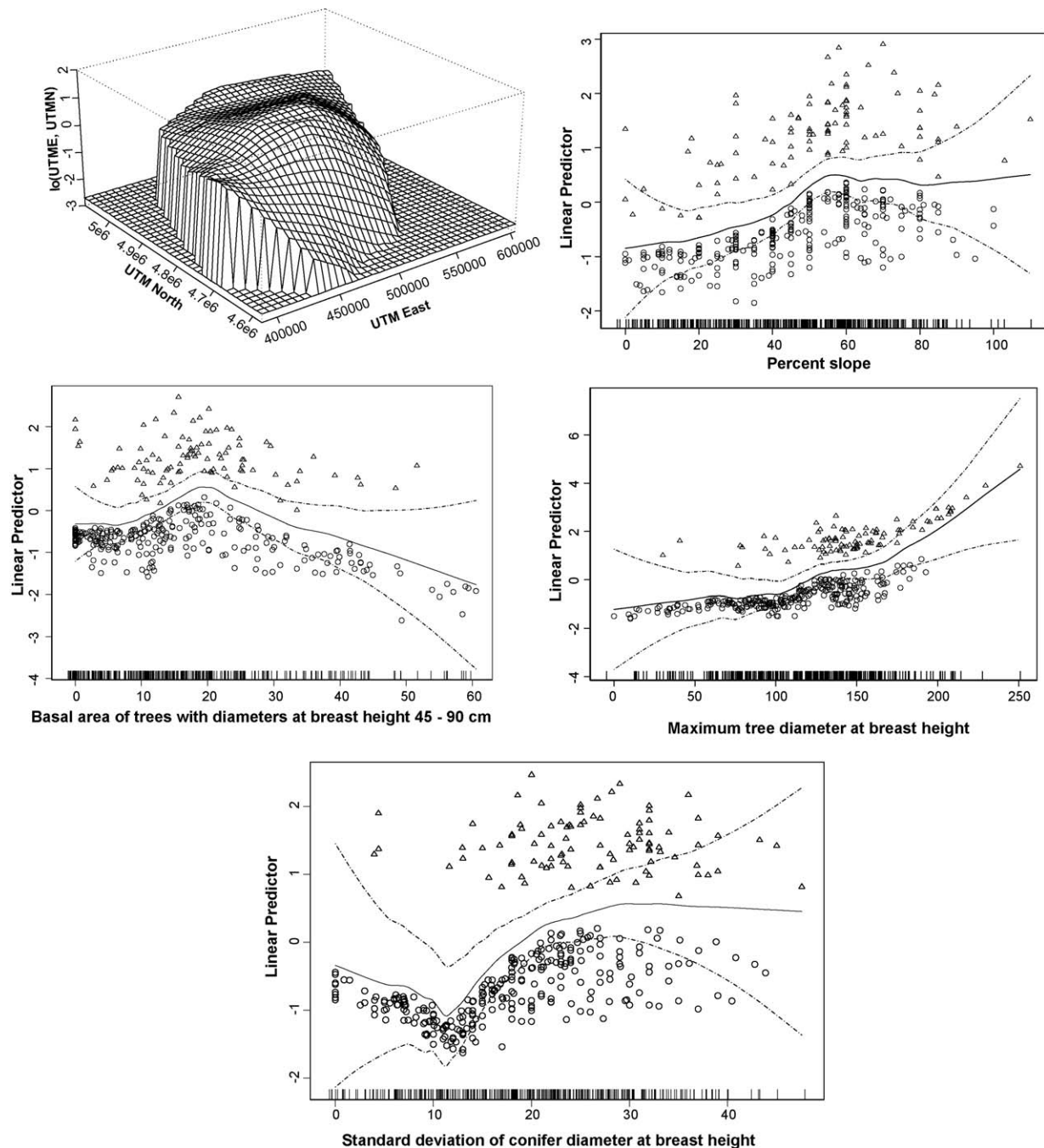[a] Variables included in best predictive model.

Fig. 2. Shape of estimated nonparametric function (solid line) and 95% confidence intervals (dotted line) for the best predictive model. These functional forms describe the relationship of each independent variable to the probability of red-tree vole nest presence given the inclusion of all other variables in the model. Vertical tick marks on the *x*-axes represent explanatory variable values for each plot. *y*-Axis values are on the logit-scale. Circles represent plots at which tree vole nests were not found, triangles represent plots at which tree vole nests were found. For interpretation, circles and triangles should not visually be projected to the *y*-axis, but to the *x*-axis.

occupancy and each variable was generally non-linear (see Fig. 2), with maximum tree dbh being the closest to linear. There was no spatial autocorrelation in the residuals of the best model (Moran's $I = 0.024$, $P = 0.40$). The best model discriminated well between plots with and without RTV nests (Fig. 3). With a Po cut-off point of 0.25 to classify plots as being occupied (≥ 0.25) or unoccupied (< 0.25), the best model correctly predicted 84.4% of occupied plots and 76.6% of unoccupied plots. Cohen's kappa, with a cutoff point of 0.25, was 0.525, suggesting that the model's predictive accuracy was 52.5% better than would be expected by chance. The AUC for the best model was 0.866, again suggesting good model prediction. On ∼86% of occasions, a random selection of the plots with RTV

nests detected will have a greater Po than a random selection of plots at which RTV nests were not detected.

Cross-validated results were quite similar to those achieved using the entire data set. Correct classification rates of the cross-validated (test) data were 85.26% for plots with RTV nests, and 70.81% for plots without RTV nests. Cohen's kappa for the cross-validated (test) data was 0.480, and the AUC for ROC curves was 0.7981. Each of these evaluation measures suggested that our model was relatively robust, and a good predictor of the presence/absence of RTV nests.

Strength of selection was strongly positively correlated with mean Po for each of the 10 bins ($r^2 = 0.943$). The power function
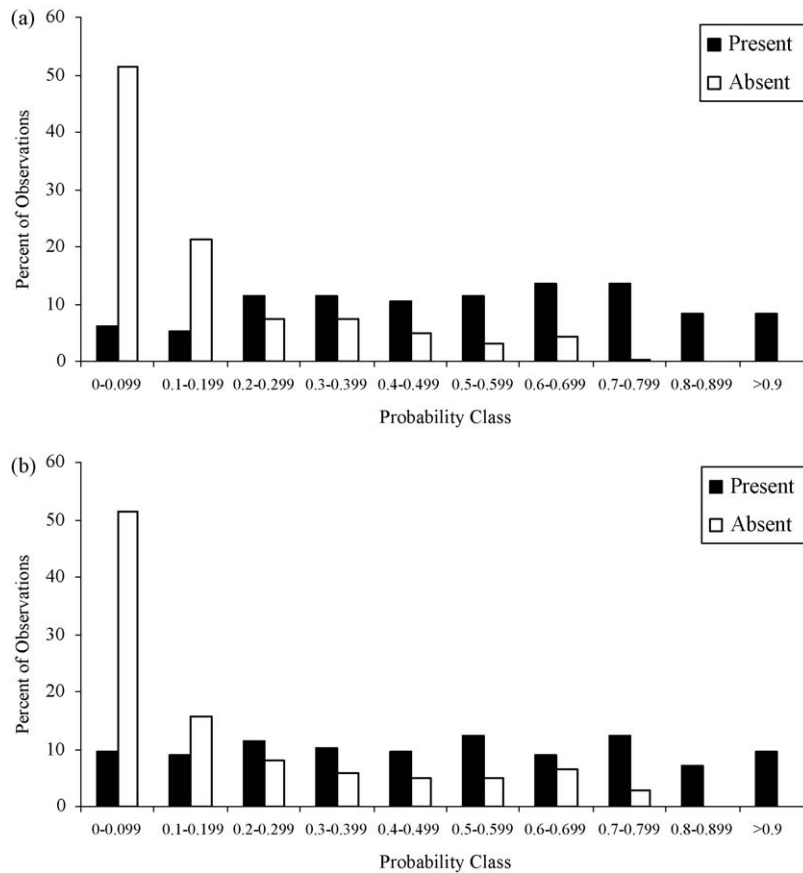
Fig. 3. Distribution of predicted probabilities of red-tree vole nest presence, by presence or absence of nests, from the best model. (A) Full data set. (B) Cross-validated data set.

$y = 0.1403 \times x^{1.6543}$ best described the relationship between strength of selection (y) and mean value of each of the 10 Po bins (x). Plots whose Po value fell within the lowest- and second lowest-ranking bins were used 7.6 and 3.4 times *less* than expected based on their areal extent in the landscape, respectively. Conversely, the second highest and highest value bins were used 5.6 and 7.0 times *more* often than expected based on their areal extent, respectively.

3.2. Red-tree vole associations with reserved lands

Mean Po values were significantly greater in reserved land plots ($\bar{x} = 0.253$, SE = 0.011) than in non-reserved land plots ($\bar{x} = 0.177$, SE = 0.010) ($t = -5.093$, $P = 4.2 \times 10^{-7}$).

More FIA/CVS plots were classified into the lowest ranking Po bin than any other bin, but a larger percentage of non-reserve plots were classified in this bin than reserved plots (53.3% vs. 42.5%). Nearly two times more reserve land plots were classified in higher ranking bins than non-reserve land plots, with 11.16% of non-reserve plots in bins with Po values >0.5, and 20.74% of reserve plots within those same bins.

Mean values for most biotic variables we considered increased with increasing bin rank (Table 2). Canopy cover of conifers was, on average, high at all plots, whereas canopy cover of hardwoods was higher in lower ranking bins than higher ranking bins. Number of nests detected was not randomly distributed among the four Po bins ($\chi^2 = 147$, $P = 3.2 \times 10^{-27}$). This highly significant difference was due primarily to the lowest ranking Po bin having many *more*

Table 2

Mean and SE of biotic variables in FIA/CVS plots classified into four probability of red-tree vole nest occupancy (Po) bins.

Po bin	0–0.249		0.25–0.499		0.5–0.749		>0.75	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Maximum tree dbh (cm)	96.2	2.49	140.41	2.72	153.58	2.34	194.66	7.22
Mean dbh of largest five trees (cm)	74.91	2.23	115.42	2.81	131.15	2.49	162.31	6.86
Mean dbh of largest Douglas fir (cm)	38.23	1.71	66.57	3.29	72.80	3.01	92.59	9.28
Maximum Douglas fir dbh (cm)	85.42	3.00	135.98	3.00	151.42	2.31	190.74	7.72
Mean dbh of conifers (cm)	34.03	1.18	42.58	1.88	44.46	1.79	50.68	5.73
Standard deviation of conifer dbh (cm)	14.99	0.55	24.69	0.79	28.63	0.87	32.42	1.42
Basal area of trees (m²/ha)	39.04	1.64	51.20	2.45	58.00	2.47	65.84	4.62
Basal area of trees >45 cm dbh	21.05	1.47	38.31	2.38	46.61	2.52	54.09	4.22
Basal area of trees 45–90 cm dbh	14.90	1.04	19.62	1.37	18.76	1.08	18.96	1.57
Basal area of trees >90 cm dbh	6.15	0.66	18.69	1.88	27.85	2.15	35.13	4.58
Mean tree age (years)	114.80	4.52	148.21	7.19	147.26	9.17	166.24	18.39
Percent conifer canopy cover	89.59	0.98	94.04	1.18	95.38	0.86	96.89	0.84
Percent hardwood canopy cover	9.17	1.53	10.01	2.40	5.02	1.38	6.78	3.36

plots with no RTV nests, and *fewer* plots with 1, 2–3, or ≥ 4 nests than expected; and to the second highest and highest-ranking Po bins having *fewer* plots with zero nests detected and *more* plots with 1, 2–3, and ≥ 4 nests detected than expected. Under a random distribution of nests among Po bins, the highest ranking Po bin was expected to have 13 plots with zero nests detected; in that bin there were no plots with zero nests detected.

4. Discussion

For many species of rare or sensitive species basic conservation and management questions include: (1) do existing reserves adequately conserve the species' habitat, and (2) in actively managed portions of the species range (inside and outside of reserves), how does (or could) management increase or decrease an area's suitability for the species? We have provided a quantitative evaluation of both questions. This study represents the most *intensive* and *extensive* evaluation of RTV habitat associations conducted to date, and the only evaluation of value of reserved lands to RTV habitat. This, coupled with our best model's good-to-excellent predictive ability, allows for drawing inferences to most of the geographic range of the species, with the possible exception of the northern Coast Ranges and northern Cascades of Oregon. Although, no sampling took place on private lands during this study, sampled plots encompassed a wide range of ecological gradients, and therefore likely included representations of most conditions which existed on private lands.

Because part of the field sampling protocol included climbing a series of five relatively large diameter trees if the canopy view was obscured, there could have been some bias in terms of plots without trees climbed having false negatives (recorded as having no RTV nests, when they in fact had at least one). In retrospect, five random trees in all plots should probably have been climbed. However, in plots where both ground surveys and tree climbing occurred the actual false negative rate from ground surveys alone was only 6.04%, and thus this potential bias was quite minor and has a negligible effect on our findings and conclusions.

We found RTV nests strongly associated with old-growth/late-seral forest conditions. Our findings suggest that optimal RTV habitat (i.e., habitat classified into the highest-ranking bins; Fig. 3) was quite rare overall. The habitats represented by the highest and second-highest ranking bins were used 7.0 and 5.6 times *more than* expected based on their areal extent, respectively. In contrast, although RTV nests were found in plots with early seral forest conditions, such areas were selected much less than expected based on their areal extent (e.g., the lowest and second-ranking bins were used 7.6 and 3.4 times *less than* expected, respectively).

The inclusion of UTM coordinates in the best model indicated a strong spatial effect on the distribution of RTV nests. To determine whether UTM coordinates were actually representing some unevaluated abiotic factors, we replaced UTM coordinates with mean annual precipitation and mean annual temperature, but that *post-facto* model would not have ranked in the top 30 if it had been an *a priori* model. Whether the spatial effect was a function of the study area's deeper biogeographic history (see Miller et al., 2006), more recent anthropogenic effects (primarily timber harvest during the past 100 years), RTV population processes, or some combination of these is unknown.

Because of strong correlations among many late-seral/old-growth variables (e.g., volume of large downed wood, maximum tree diameter, basal area of trees >90 cm dbh), only one of those measures (maximum tree dbh) is represented in our best model. Standard deviation of conifer dbh was used as a predictive variable owing to it representing the continuum from even-sized to uneven-sized trees in a plot. Uneven size distributions are characteristic of late-seral/old-growth forests, and RTV nest Po increased with increasing variation (SD) in conifer diameters up to ~30 cm, after which Po was relatively stable. The association of RTV with late-seral forest conditions is evidenced from univariate differences (e.g., large downed wood, basal area of trees >90 cm dbh, mean dbh of Douglas fir, SD dbh of conifers) found between plots with and without nests (Table 1). However, not all RTV nests were detected within plots containing late-seral/old-growth habitat, as consistent with other RTV studies (Taylor, 1915; Howell, 1926; Benson and Borell, 1931; Maser, 1966; Carey, 1991; Thompson and Diller, 2002; Swingle, 2005).

The positive relationship between RTV Po and slope could be biological in nature (though we cannot surmise what, biologically, could account for it) or related to patterns of timber harvesting during the past 100 years. That is, harvesting likely occurred first in alluvial floodplains along river and stream corridors due to both the presence of large trees and proximity to water for transporting logs. Steeper areas may have simply been avoided, becoming *de facto* refugia, rather than areas selected by RTV because of their steepness.

Po of RTV nests showed a quadratic relationship with basal area of trees with dbh = 45–90 cm. The presence of some medium sized trees (highest Po corresponded with approximately 20 m^2/ha of basal area of trees with dbh = 45–90 cm) in plots with RTV nests is consistent with uneven size distributions of late-seral/old-growth forests. Lastly, the inclusion of maximum tree diameter in the best model and the approximately linear and positive (Fig. 2) relationship between Po and maximum tree diameter adds further support to the contention that RTVs are associated with late-seral and old-growth forests. Other researchers reported that the number of RTV nests per tree increased with tree dbh (Carey, 1991; Gillesberg and Carey, 1991), and that nest densities increased with dbh (Jones, 2003) and stand age (Biswell and Forsman, 1999; Thompson and Diller, 2002). Huff et al. (1992) found 67% of tree vole nests in stands >300 years of age, with a range from 62 to 525 years. In our sample, only two plots with RTV nests had maximum tree diameters < 50 cm, whereas 91 of 96 RTV-occupied plots had maximum tree diameters >90 cm.

Most researchers who have evaluated RTV habitat associations have pre-categorized habitats into various age classes or structural types (e.g., old-growth, mature, young). Nearly all found RTV to be disproportionately associated with old-growth and/or mature forests (Gomez and Anthony, 1998; Meiselman and Doyle, 1996; Gillesberg and Carey, 1991; Corn and Bury, 1991). However, Swingle (2005) and Maser (1965) reported finding many occupied RTV nests in young forests in Oregon. Similarly, Thompson and Diller (2002) evaluated *A. pomo* abundance in redwood-dominated forests under intensive, private, timber management in coastal northwestern California. Their study area contained little-to-no old-growth forests, yet tree voles were found in all but the youngest stands (10–19 years) and tree vole nest density increased with stand age (Thompson and Diller, 2002). During our study, RTV were found in forests with varying structures, but RTV's disproportionately selected areas with older forest characteristics.

Prior to ours, no RTV studies have provided predictive habitat models with widely available habitat data. For example, Meiselman and Doyle (1996) used a series of project-specific variables measured in 0.04 ha plots to develop a discriminant function model to classify plots with and without RTV nests. Zielinski et al. (2006) and Welsh et al. (2006) discussed the value of using the routinely collected FIA data for developing wildlife habitat association models, because (among other reasons) variables used for such models are available at all FIA plots within USDA Forest Service (USFS) and Bureau of Land Management (BLM) management jurisdictions. Additionally, most FIA/CVS data contain variables that are directly interpretable by managers (e.g., basal area of conifers, basal area of trees >90 cm dbh).

Our results can be considered the first large-scale baseline assessment of the distribution of RTV habitat quality throughout its range on public lands. As CVS/FIA plots are revisited over time, plot-level variables can be put into our best model to evaluate how habitat quality changes in distribution and abundance. For example, we found reserve and non-reserve lands to have mean RTV nest Po of 0.253 and 0.177, respectively. Because reserve lands are likely to be managed differently (especially with regard to maintaining or enhancing late-seral/old-growth forest characteristics) than non-reserve lands, we should expect the difference in mean Po to increase over time. Furthermore, land managers can evaluate the change in quality of RTV habitat on lands under their jurisdiction. The generalized approach presented here can also be applied to many other species (e.g., see Welsh et al., 2006, Zielinski et al., 2006; Dunk et al., 2004). This approach requires a larger up-front investment. However, if good predictive models can be developed there are likely to be longer-term cost savings when monitoring a species' habitat distribution and quality over time.

Those wishing to evaluate RTV habitat quality can also use our best model to make predictions about relative habitat value to RTVs in areas where they have estimated the predictor variables from our model. However, strict management based on the outcome of our best model would be a mistake. That is, our best model is a representation, and allows for prediction, of the presence or absence of RTV nests based on the totality of conditions at the sample locations. Our best model detected a strong signal of important plot features. That signal, however, is not the complete representation of RTV habitat, nor should the variables in the best model be solely used to evaluate RTV management or for mitigation at the site level. Land managers wishing to forecast effects of proposed management actions on RTV would be better served by considering the univariate differences in variables at plots classified into different Po bins (see Table 2). In Table 2 we have provided mean (and SE) values for plot variables that land managers can gauge and control during many of their activities. For example, mean basal area of trees >90 cm dbh increased from 6.15, to 18.7, to 27.9 to 35.1 m²/ha when going from the lowest to the highest ranking bins (Table 2). The same pattern can be seen in maximum tree diameter, mean diameter of the five largest trees, maximum diameter of Douglas fir, mean tree diameter, standard deviation of conifer diameter, total basal area, and basal area of trees >45 cm dbh. Furthermore, we found that more trees with vole nests were likely to be found in higher ranking Po bins than lower ranking bins; supporting the idea that Po values derived from presence–absence data are, in this case, related to abundance as well.

Our evaluation of RTV habitat associations occurred only at the 1-ha scale, therefore caution is warranted in interpreting our data. Tree vole distribution may be, in part, a function of dispersal limitations as they appear intolerant of extensive habitat fragmentation (Bailey, 1936; CA Fish and Game, 1986; Carey, 1991; Huff et al., 1992; Biswell and Forsman, 1999; Biswell et al., 2000). Huff et al. (1992) stated that RTV are the "most vulnerable arboreal rodent to local extirpations resulting from habitat loss or fragmentation." An Oregon RTV suitability index model suggested a minimum stand size of 29.55 ha required for occupation (Huff et al., 1992). If this holds true, connectivity of sites at scales greater than 1 ha is important. Our modeling approach and scale did not evaluate habitat fragmentation, and thus is likely missing phenomena from larger scales that influence RTV distribution. However, the strong spatial effect in our model could be a manifestation of barriers to RTV dispersal (including habitat fragmentation). Multi-scale habitat evaluations (Martin and McComb, 2002) could help elucidate such relationships. Due to the somewhat aggregated nature of high-quality RTV habitat and the fact that RTV are known to have aggregated distributions

within localized areas (Taylor, 1915; Meiselman and Doyle, 1996; Adam and Hayes, 1998), RTV management and/or conservation-related activities are likely to have more positive effects on RTV if they are adjacent to currently occupied sites/stands. Under the NWFP, riparian reserves were created along river and stream courses to both help aquatic species and to facilitate connectivity for terrestrial species. The degree to which riparian reserves actually provide connectivity for RTV is unknown. Of particular interest now is the relationship between Po of RTV (from our best model) and some measure of RTV fitness, along with the association of RTV fitness to habitat. Until then, our findings suggest that the highest quality areas for RTV nests (those most strongly selected) are forests containing old-growth characteristics; areas with more basal area of large diameter and older conifers.

Acknowledgments

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